

## **Cementation in *Cleidothaerus albidus* (Lamarck, 1819) (Bivalvia: Anomalodesmata: Pandoroidea)**

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### **Abstract**

The pandorid anomalodesmatan *Cleidothaerus albidus* cements to hard substrata by the anterior half of the middle mantle folds. Cementation begins after settlement of a lecithotrophic larva during the dissoconch stage (at a mean height of 1.2 mm), presumably after a brief period of byssal attachment. The aragonitic shell comprises a thick inner nacreous layer, with 'chalky deposits', and a thin outer prismatic layer. The persistent periostracum is relatively thick. It is bi-layered with the outer layer being thinner (1-2  $\mu\text{m}$ ) on the right cemented valve than the 'upper' left valve (10  $\mu\text{m}$ ). The inner layer, secreted by the outer component of the periostracal groove, is probably more mucoid. There are no obvious differences in the character of the right valve periostracum between areas of cementation and non-cementation. An extra-pallial cement was discovered under some parts of the attached valve where it had accumulated in 'valleys' in the substratum, providing the necessary smoothing to allow adhesion. The cement was mainly unmineralised but in some patches showed spherulitic growth of (?) aragonite.

*Cleidothaerus albidus* shows Type B pallial fusion, i.e. fusion of the inner and inner surfaces of the middle mantle folds. Significantly, no arenophilic glands were observed, however, we did identify a large gland within the mantle cavity of the right lobe that was restricted to the anterior portion, i.e. the part of the mantle directly involved with cementation. This structure comprises two types of secretory cells. Since the gland was restricted to only those parts of the mantle that were involved in cementation, we suggest that it may be responsible for the production of the cement that drains, under gravity, to exit the mantle cavity at the pedal gape, coating the attaching periostracum.

### **Introduction**

The sub-class Anomalodesmata, as its name implies, is an assemblage of disparate species and genera that are contained within 14 extant and 8 extinct families, and constituting approximately 15% of the current familial diversity of the Bivalvia. Most anomalodesmatan families, however, are small, comprising only a few genera most of which also contain a small number of species. Moreover, many anomalodesmatan taxa are highly specialised occupying narrow niches with restricted geographic distributions and most are, therefore, considered "rare". These small disparate families are all that remain of a sub-class which was abundant and widespread throughout the Palaeozoic and Mesozoic (Runnegar, 1974). Morton (1981) believes that the decline in abundance and distribution of this ancient group was due to increasing competition from the more generalist Heterodonta and Pteriomorpha which have become the predominant bivalve space occupiers in today's marine environment, for example the mytilid mussels on rocky shores and venerid and cardiid burrowers in soft sediments.



The relationships of the once successful anomalodesmatan bivalves to the small specialised families which survive are obscure, masked by apparently multiple examples of convergent and parallel evolution (Morton, 1981, 1985; Harper et al., 2000). Morton (1981, p. 53) has likened the extant members of the sub-class to "the outermost twigs of a tree of which most of the main branches, stem and roots have died out". The surviving twigs of the anomalodesmatan tree span a wide range of bivalve morphological diversity. In addition to burrowers and endo- and epibyssate taxa, there are those which build adventitious tubes (Clavagellidae), a range of species contained within the three (Cuspidariidae, Poromyidae, Verticordiidae), probably four (Parilimyidae), predatory families in the deep sea, and nestling (Lyonsiidae) and boring (Clavagellidae) taxa. Additionally, members of three families [species of *Clavagella* (Clavagellidae), *Myochama* (Myochamidae) and *Cleidothera* (Cleidotheridae)] have evolved the ability to cement one of their valves to hard substrata. Cementation appears to have arisen independently in each of these families and, although small and less important than the better known pteriomorph cementers, e.g. oysters, they provide an interesting insight into the polyphyletic evolution of this habit in the Bivalvia (Yonge, 1979; Harper, 1991).

The process of cementation has been most intensively studied for ostreid oysters, where it commences early in ontogeny, e.g. 18 days after egg fertilization in *Ostrea edulis* Linnaeus (Waller, 1981). In the initial stages the pediveliger attaches to its substratum by means of a tanned mucopolysaccharide secreted by the foot and inner mantle fold (Cranfield, 1973a,b,c, 1975). Later, however, a crystalline calcium carbonate cement is developed between the periostracum and the substratum (Harper, 1992, 1997). The spherulitic nature of this cement resembles those secreted under dominantly physico-chemically controlled conditions rather than direct biotic control (Constanz, 1986).

Although there has been considerable research into the evolution of the cemented habit in the oysters, relatively little is known about how and why the cementing clades of Anomalodesmata have arisen. It is also interesting because the habit arose in anomalodesmatans during the late Cenozoic, compared to a late Palaeozoic/early Mesozoic origin for the larger and better known cementing clades (Harper, 1991). Morton (1984) suggested that clavagellids attach their left valve to an adventitious tube by secretions from arenophilic glands around the siphons. Certainly, arenophilic glands are widely used amongst non-cementing anomalodesmatans to attach small sand grains and other detritus to the external surface of their shells, e.g. *Lyonsia* (Prezant, 1979) and *Entodesma* (Morton, 1987). A recent study of attachment in *Myochama anomioidea* has demonstrated the presence of a homogenous layer of cement between its shell and the substratum (Harper and Morton, 2000). This cement was composed largely of a non-mineralised material although there was evidence that it did have a calcareous component. Members of the Myochamidae lack arenophilic glands, but it seems probable that other mantle glands are responsible for the secretion of this cement. Despite concerted effort, however, that investigation detected no sign of these.

This study investigates cementation in another exclusively Australasian (both in Australia and New Zealand) anomalodesmatan family, the



Cleidothaeridae Hedley, 1918 (Pandoroidea). The family is monotypic, with *Cleidothaerus* Stutchbury, 1830 appearing first in the Lower Miocene (Beu and Maxwell, 1990). Although there are three recorded extant species, i.e., the type, *C. albidus* (Lamarck, 1819), *C. maorianus* (Finlay, 1827) and *C. plicifera* (Odhner, 1917), it is likely that the first two are synonymous (Morton, 1974) and the taxonomic validity of the latter is unclear.

*Cleidothaerus* cements by its robust, coiled, right valve to hard substrata in the intertidal zone and subtidally to depths of 40 m (Prezant, 1998). There is a pronounced tendency to attach to upward facing surfaces. The combination of the cemented habit and coiled morphology gives a convergent similarity to the heterodont Chamidae. The anatomies of the three putative species have been investigated (Hancock, 1853; Odhner, 1917; Morton, 1974), while Yonge and Morton (1980) described the ligament during their discussion of the pandoroid hinge. This study investigates *Cleidothaerus albidus* and concentrates on its cemented habit, specifically the timing of its attachment and the method by which it adheres.

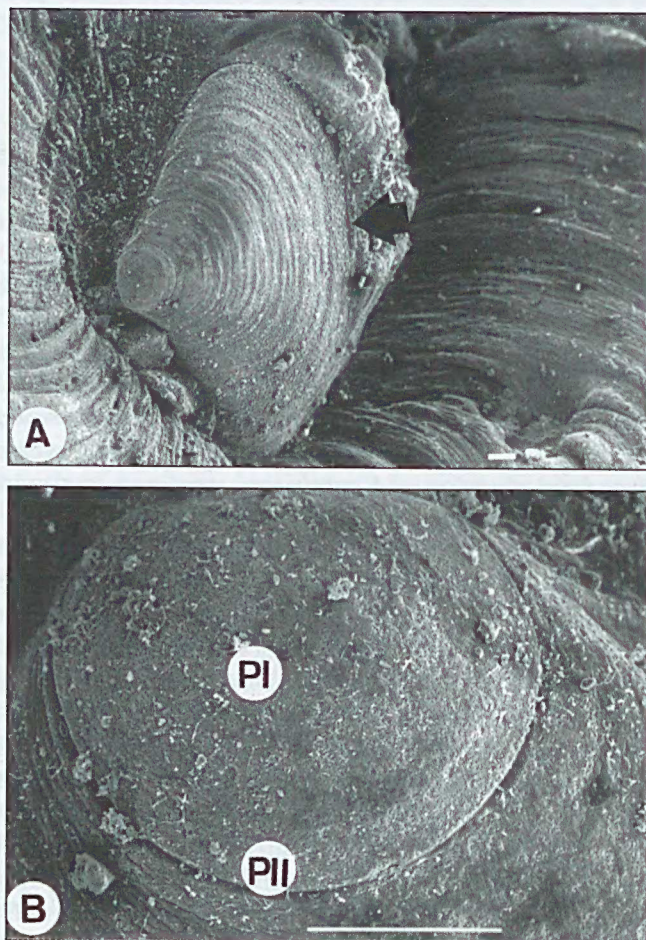
### Materials and Methods

All available specimens of *Cleidothaerus albidus* in the collections of the Natural History Museum (London), the Australian Museum (Sydney) and the National Museum of Victoria (Melbourne) were examined. Additionally, a number of specimens, collected in 1994 by P.A. Hutchings and R. Bieler, from Fairlight, North Harbour, Sydney, where they were attached to a coarse sandstone (6–9 m depth) were also examined. Particular attention was paid to the 'lower' right valve. Although often obscured by both coiling and adherent substratum, 21 individuals showed details of the earliest part of the shell thereby allowing the size at which cementation occurred to be determined using vernier calipers (to the nearest 0.1 mm). One specimen, which showed a particularly clear nepioconch, free from abrasion and encrusters, was examined with a scanning electron microscope (JEOL 820), in order to study the larval shell.

The nature of the attachment was studied by selecting individuals still attached to their substrata. As noted by Harper (1992, p.39), attachment is best studied in individuals that have grown on an homogeneous substratum which is easy to distinguish and where the surface is not complicated by fouling epibionts. This is, obviously, best achieved by rearing the spat and allowing them to settle on man-made substrata such as glass. Although this has not been possible for this study, it was found that the coarse quartz-rich sandstones which are a frequent substratum, particularly of individuals collected around Sydney, do offer a reasonable alternative, although precise details are often complicated by the presence of bryozoans and coralline algae. Selected attached valves were set in epoxy resin and sectioned along the valve height, whilst others were made into petrological thin sections. The cut surfaces of both blocks and thin sections were polished with carborundum powder, etched with 1% hydrochloric acid for 25 seconds and then examined using SEM. Additionally, the undersides of the right valves of several individuals that had adhering substrata were also investigated by SEM. Elemental compositions were ascertained using elemental dispersive X-ray microanalysis (EDAX) with the LINK AN 10 000 system.



In order to examine anatomical detail, we studied three individuals of *Cleidotheraerus albidus*. One specimen (approximately 40 mm in shell height) from the Abrolhos Islands, Western Australia (collected by J.D. Taylor and E.A. Glover), attached to the outside of a pectinid shell, was sectioned in its entirety at 6  $\mu\text{m}$  and alternate slides stained in either Ehrlich's haematoxylin and eosin or Masson's trichrome. The right and left mantle lobes only of two other specimens from the collections of the Australian Museum, C387327 from Exmouth Gulf, Western Australia and C387325 from Fraser Island, Queensland, with shell heights of 28 and 69 mm respectively, were also stained and sectioned in the same manner. The precise fixation history of these three specimens are unknown but it seems probable that they were initially fixed in formalin prior to preservation in ethanol. Comparisons were made between these sections and those of *C. maorianus* earlier reported upon by Morton (1974).



**Figure 1**

Scanning electron micrographs of the earliest part of the right valve of *Cleidotheraerus albidus*. **A.** Pre-attachment valve, change to a cemented life habit at the arrow. Scale bar = 100  $\mu\text{m}$ . **B.** Detail of the prodissoconch. Scale bar = 10  $\mu\text{m}$ . (For abbreviations see p.13).



## Results

Scanning electron micrographs of the earliest formed parts of the right valve of an individual of *Cleidothaerus albidus* revealed details of the prodissoconch and the pre-attachment part of the shell (Fig. 1A and B). The clearly defined, unornamented prodissoconch I (height = 175  $\mu\text{m}$ , length = 210  $\mu\text{m}$ ) is fringed by a narrow (25  $\mu\text{m}$ ) band of the prodissoconch II which has commarginal growth lines (Fig. 1B). The transition between the prodissoconch and dissoconch is also clearly defined. The early portion of the dissoconch is also ornamented with commarginal ridges and furrows, and has a hexagonal surface pattern. It seems likely, from similarity of scale, that this hexagonal pattern reflects the ends of the underlying prismatic shell layer.

The onset of cementation occurs within the dissoconch stage, i.e. much later than oysters (Yonge, 1979) and is marked clearly by a disruption of the idiomorphic shell growth to take up substratal irregularities (Fig. 1A), the most prominent of which are taken up as xenomorphic ornament on the unattached left valve. The mean shell height at which cementation occurs in *Cleidothaerus albidus* was measured to be 1.2 mm ( $n = 21$ ;  $sn-1 = 0.2$ ). There is no sign of a byssal notch.

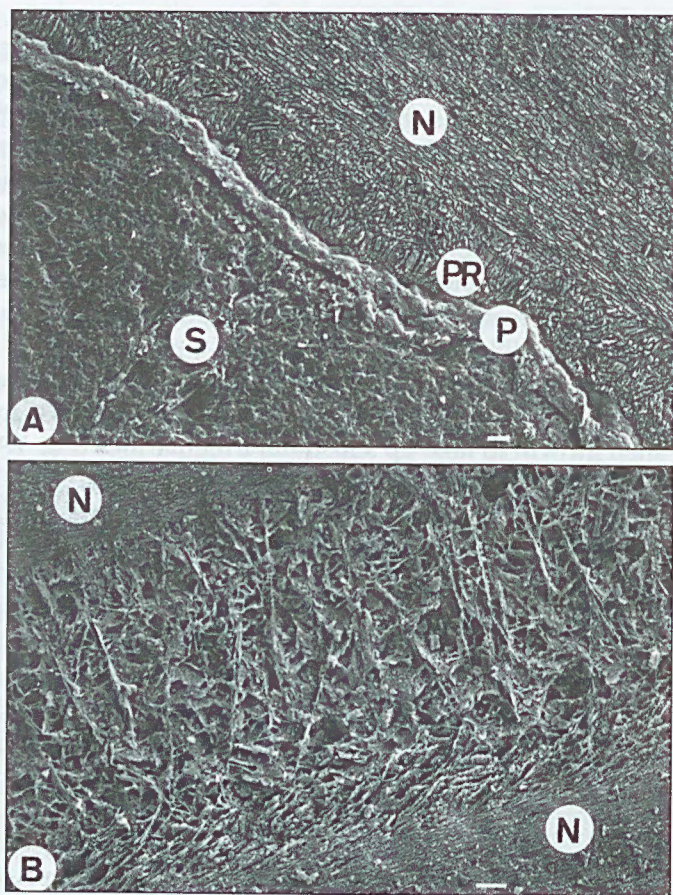
Individuals of *Cleidothaerus albidus* attach to the substratum by the anterior face of the right valve. In most cases the attachment scar is extensive although in some individuals areas of the valve are elevated from the substratum. These non-cemented areas retain idiomorphic shell ornament and show no signs of cement adhering to the outside of the periostracum.

## Shell microstructure

As recorded by Taylor et al. (1973), the calcareous part of the valves of *Cleidothaerus albidus* is wholly aragonitic, the bulk of which comprises nacre but with a thin (up to 20  $\mu\text{m}$ ) outer prismatic layer which is often not easily discernible (Fig. 2A). This study has also revealed the presence of patches of opaque, white material within the nacre. Investigation by SEM showed that these patches display an open, bladed, crystal texture, with individual blades aligned perpendicular to the growth surface (Fig. 2B). This microstructure is strikingly similar to the 'chalky deposits' recognised in a variety of oyster taxa (Korringa, 1951; Chinzei and Seilacher, 1993; Malchus, 1998).

The external surface of the shell is covered by a red-brown periostracum, which is persistent over all but the most abraded regions. The surface of the periostracum is wrinkled and there was no evidence of either the calcareous spicules or spinules which have been observed in a wide range of other anomalodesmatan taxa (Carter and Aller, 1975). Investigation of the inner surface of the periostracum did not yield any sign of the well-formed hexagonal craters, which correspond to pyramidal bosses on the outside of the shell, reported upon for *Myochama anomioidea* by Harper and Morton (2000). SEM of sections through the periostracum covering non-cemented parts of the valve revealed that it has an average thickness of 15  $\mu\text{m}$ , but displays some variability. There was no evidence either of layering or other internal structure using SEM, however, as described later, stained histological sections showed it to be bi-layered.





**Figure 2**

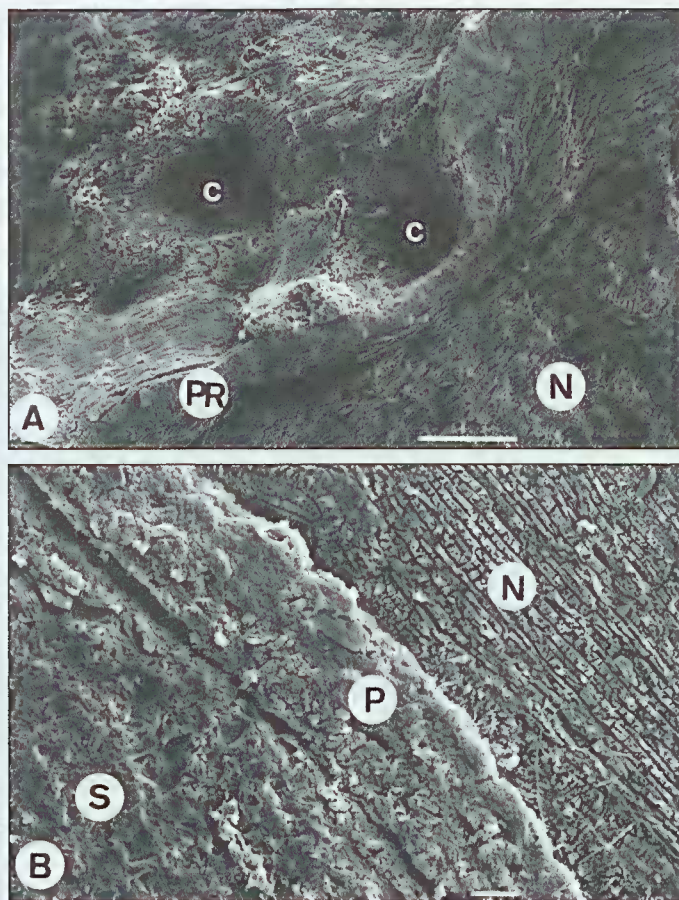
Scanning electron micrographs of the microstructure of the right valve of *Cleidothaerus albidus*. A. Shell microstructure of the right valve adhering to a sandstone substratum. B. Chalky microstructure within the nacreous layer. Both scale bars = 10 µm.

(For abbreviations see p.13)

### Cement

During the cementing phase, the anterior face of the right valve follows closely topographic irregularities in the substratum. Figure 3A shows the extent to which the morphology of individual sand grains is reflected in the outer prismatic shell layer. The implication of this is that the periostracal sheet is capable of intricate folding and is applied closely to the substratum. There is no sign that either the thickness or structure of the periostracum is different during cementation as it is in *Etheria elliptica* (Grégoire, 1974) and *Myochama anomioidea* (Harper and Morton, 2000). Detailed investigation of the association between the periostracum and substratum shows that it hugs the surface of the sand grains with no obvious material between (Fig. 3B). There are, however, 'valleys' in the substratum, for example, between adjacent sand grains, that are too acute for the periostracum to follow. In these instances, the periostracum bridges the 'valley' and there is an accumulation of cement below it.





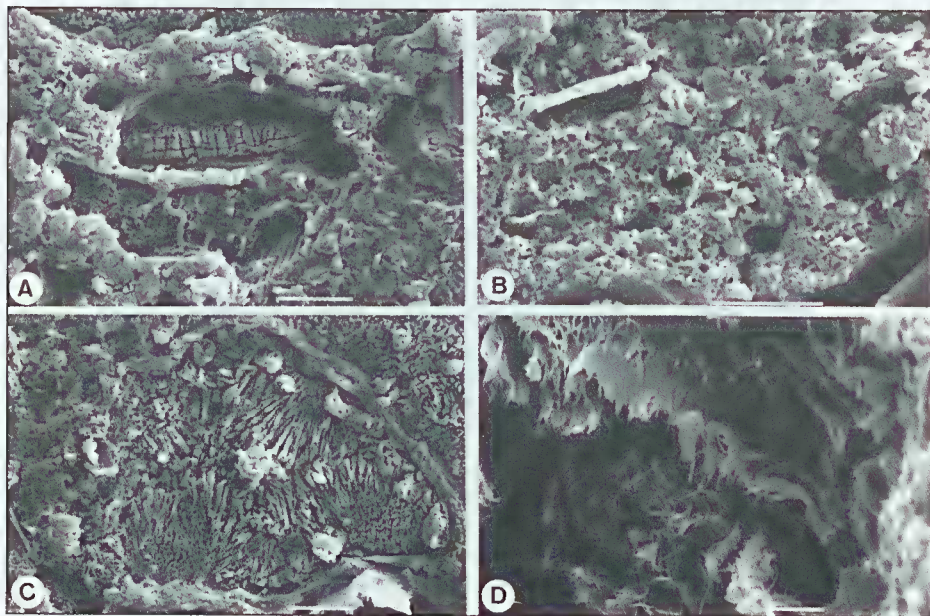
**Figure 3**

Scanning electron micrographs of attachment of *Cleidotheraerus albidus*. **A.** Attachment scar viewed from the underneath of a specimen that had been prised away from its substratum, revealing craters embossed into the prismatic shell layer where the valve has moulded over individual sand grains. Scale bar = 100  $\mu\text{m}$ . **B.** Close up of the relationship between the periostracum and a sand grain with obvious intervening cement layer between them. Scale bar = 10  $\mu\text{m}$ . (For abbreviations see p.13).

The extra-periostracal nature of the cement is confirmed by the presence of foreign material trapped within it, some of it recognizable as fragments of molluscan shell (Fig. 4A). Most of the cement has an open, spongy, texture (Fig. 4B), although some of it is composed of fine sheets (Fig. 4D) not dissimilar to the mucous ones illustrated by Taylor et al. (1999, figs 6A, C and D). It is not clear whether the spongy areas contained scattered crystals that have been lost during acid preparation of the specimens. EDAX analysis of areas free of obvious foreign inclusions, and distant from adjacent shell material, revealed that calcium (nor magnesium or strontium) was not present in the spongy areas of cement. This suggests that these areas are not mineralised, although it may be true that small, scattered crystals could have been removed during acid etching. There are, however, occasional areas of spherulitic crystal growth



(Fig. 4C) which are not obviously either trapped inclusions or parts of epibionts overgrown by the cleidothaerid. The crystals associated with the spherulites are acicular, up to 15  $\mu\text{m}$  long and < 1  $\mu\text{m}$  wide. Their morphology suggests that they are probably aragonitic, but the minute volumes involved prohibit the extraction of material for X-ray diffraction analysis. The growth of spherulites which nucleate on the bounding surfaces of the void between the shell and the substratum are reminiscent both of diagenetic growth of minerals in sedimentary rocks (e.g. Bathurst, 1975) and oyster cements (Harper, 1992, 1997).



**Figure 4**

Scanning electron micrographs of the cement of *Cleidothaerus albidus*. A. Fragment of prismatic-nacreous mollusc shell trapped within the cement. B. Homogeneous areas of cement displaying a spongy texture. C. Spherulitic growth of cement crystals. D. ?mucous sheets. All scale bars = 10  $\mu\text{m}$ .

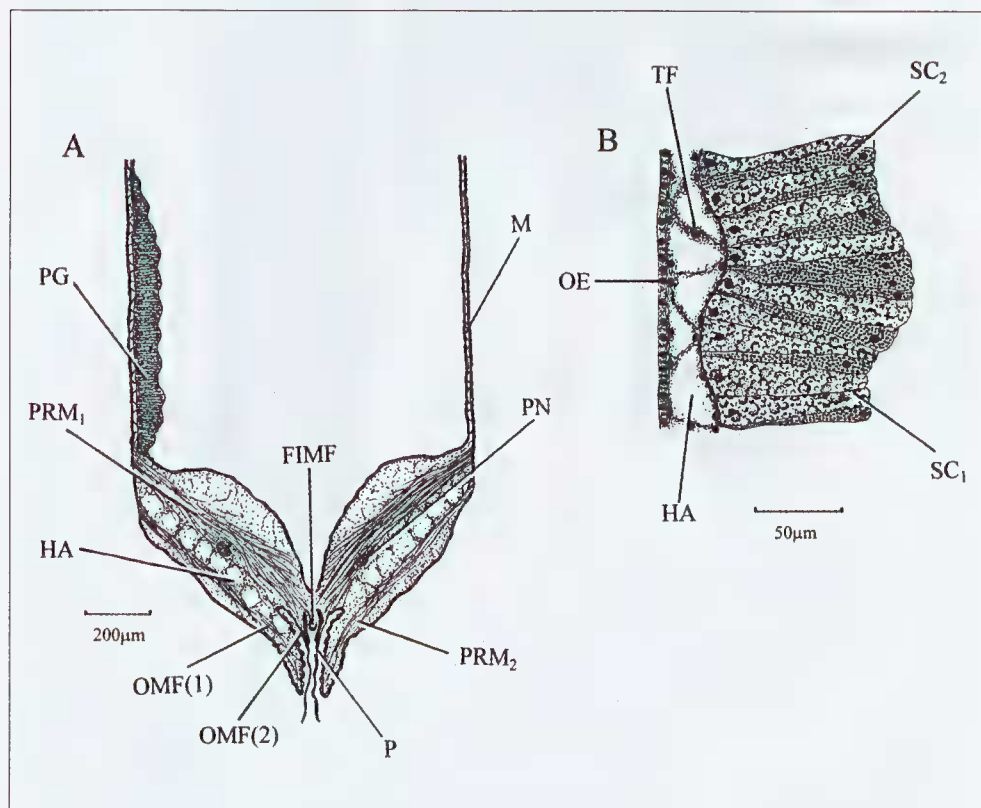
### Mantle margin

The mantle margin of *Cleidothaerus maorianus* has been described by Morton (1974) and shown to comprise the usual three folds. The situation is the same in *C. albidus* and is illustrated in transverse section in Figure 5A. Ventral mantle fusion is of the inner fold and the inner surfaces of the middle folds (FIMF), i.e. type B (Yonge, 1957). [Previously, Morton (1974) had said that such fusion in *Cleidothaerus maorianus* was of type A (inner folds only), but this is incorrect and *Cleidothaerus* thus more closely matches other anomalodesmatans in terms of the degree of mantle fusion (Harper et al. 2000).

The rather swollen ventral mantle margins mainly comprise outer folds which are divided into, larger outer (OMF(1)) and, smaller inner components (OMF(2)). Each mantle lobe contains a pallial nerve (PN) and a small haemocoel (HA). The pallial retractor muscle is divided into two components (PRM1 and PRM 2) which penetrate the inner and outer components of the outer mantle



folds, respectively. In the two smaller specimens (from the Abrolhos Islands and Exmouth Gulf) examined, a large pallial gland (PG) occupies about one half of the dorso-ventral surface of the inner surface of the anterior mantle of the right mantle lobe, above the pedal retractor muscles (and thus the pallial line). There is no similar gland in either the right mantle lobe of the larger specimen examined nor the left mantle lobe of any of the specimens. Morton (1974) did not describe any such gland in *C. maorianus* nor were any apparent when we re-investigated those sections. The gland is shown in greater detail in Figure 5B. The outer surface of the mantle (OE) comprises a cuboidal epithelium  $\sim 4\mu\text{m}$  tall. It connects by transverse fibres (TF) with the inner epithelium across a haemocoel between  $20\text{--}30\mu\text{m}$  wide. The inner surface of the mantle comprises cells  $\sim 100\mu\text{m}$  tall that can be divided into two types, both secretory. The first comprises cells with basal nuclei ( $4\mu\text{m}$  in diameter) which contain a loosely vacuolated epithelium that is eosinophilic and stains light blue in Masson's trichrome (SC1). It is probably producing mucus. Interspersed with these cells, however, are equally long secretory cells (SC2) which have apical nuclei ( $3\mu\text{m}$  in diameter). This cell type is full of small, basiphilic, spherical granules that stain dark blue in Masson's trichrome. There are no arenophilic glands in the mantle margin of either lobe.



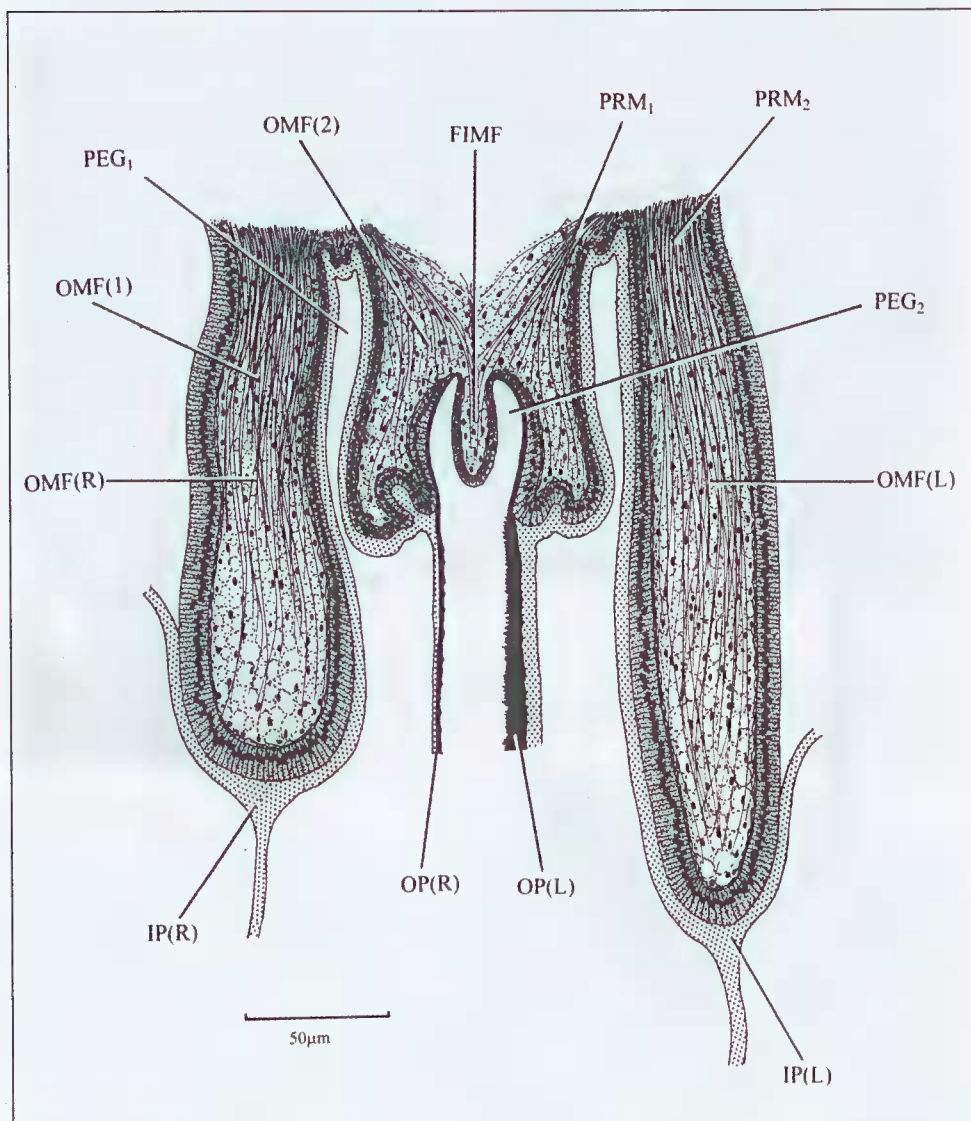
**Figure 5**

*Cleidotheraerus albidus*. **A.** A transverse section through the mantle margin, showing the pallial gland on the right mantle lobe only above the pallial line. **B.** detail of the pallial gland. (For abbreviations see p.13).



### The periostracum

As noted earlier, the periostracum of *Cleidothaerus albidus* when seen in transverse section (Fig. 6) comprises two layers, i.e. a yellow, red-staining, outer layer (OP(R), OP(L)) and a blue staining and, therefore, mucoid, thicker, inner layer (IP(R), IP(L)). Since the outer mantle fold is divided into two components, the outer layer of periostracum is secreted in the inner periostracal groove (PEG2) and is thin (1-2  $\mu\text{m}$ ) over the right lobe, that is over the cemented valve (OP(R)), but is up to five times thicker (~10  $\mu\text{m}$ ) over the unattached left valve (OP(L)).



**Figure 6**

*Cleidothaerus albidus*. A transverse section through the ventral mantle margin showing the degree of left and right fusion and the organization of the periostracum. (For abbreviations see p.13).



The inner layer of the periostracum is of equal thickness on both the left (IP(L)) and right valves (IP(R)) and is secreted against the template of the outer periostracum largely in the outer component of the periostracal groove (PEG1) and is laid down, therefore, by the majority of the inner surface of the outer mantle fold. It can be formed into a light fringe that presumably helps in sealing the shell margin when adducted. If, however, the inner periostracum is of similar structure to that of *Myochama anomioidea* (Harper and Morton, 2000) it is likely that it has a much more liquid structure than the outer layer and over which the pallial cement will be secreted to bond the right valve to the substratum. It is possibly significant that the outer periostracum of the 'free' left valve is at least five times thicker than that of the 'attached' right valve.

## Discussion

Like most Anomalodesmata, members of the Cleidothaeridae are simultaneous hermaphrodites (Morton, 1974). Comparison with the data provided by Ockelman (1965) and Berkman et al. (1991) suggests that the large size of prodissoconch I and the high prodissoconch I/II ratio of *Cleidotheraerus albidus* recorded here, indicates a lecithotrophic larval phase. The presence of prodissoconch II suggests that brooding does not take place. Morton (1974) observed *Cleidotheraerus maorianus* in aquaria spawning during the austral winter, producing larvae that settled at lengths of 0.25 mm, i.e. at a size comparable with the commencement of the dissoconch stage measured in this study. However, cementation does not proceed until the shell has at least quadrupled in size suggesting that, despite the lack of any morphological evidence, e.g. the presence of a byssal notch, the pre-cementation phase is stabilised by a few byssal threads, as are most larval bivalves (Yonge, 1962).

Adhesion between two bodies can only be achieved when they are brought close enough to be held together by electromagnetic interaction (De Bruyne, 1962). This is only possible when the two surfaces are perfectly smooth and such a condition is usually attained when an adhesive fluid is introduced between them. In his study of *Cleidotheraerus maorianus* from New Zealand, Morton (1974) was unable to detect glands, pallial or otherwise, that could secrete the attaching cement and suggested, therefore, that attachment must occur by way of a sticky layer of outer periostracum. In this study we have shown that for areas of the substratum which have no pronounced microtopography the periostracum is laid down directly on to it with no obvious modification or need for adhesive. However, where there are distinct notches and valleys within the surface of the substratum, in this case between two grains in the coarse sandstone we have identified the accumulation of cement between the attached valve, i.e. the periostracum, and its substratum. Most of this cement appears unmineralised and is similar to that identified in *Myochama anomioidea* (Harper and Morton, 2000). There are, however, scattered pockets within the cement where mineralisation has occurred.

The source of the cement is of obvious interest. The outer layer of periostracum is a solid structure and there is no means for a secretion to pass through it. Instead, it seems likely that the cement is produced by the mantle and applied to the outside of the periostracum. More specifically, we suspect



that the large pallial gland identified in this study may be responsible, since it is restricted to the anterior portion of the right mantle lobe only. It seems logical that the secretion from the right pallial gland exits the mantle cavity via the pedal gape. Since both valves are here in close apposition to the substratum, not only would any internal secretion naturally drain down in this direction but would quickly encounter the anterior margin of the valve, or at least the periostracum covering it, and thereby help to cement any new shell surface being secreted. Cement is only likely to accumulate in topographic hollows within the surface of the substratum.

Failure to locate these cement-secreting glands in *Cleidotherus maorianus* (Morton, 1974) and in one, the larger, specimen of *C. albidus* examined in this study appears problematic. Harper and Morton (2000) also failed to locate the glands responsible for the similar cement in *Myochama anomioides*. It is possible that, because none of these individuals was cementing actively at the time of death, the glands may not be developed. This is certainly true of the individuals of *M. anomioides* where the ventral valve margins had lifted away from the substratum. The ventral valve margins of the larger specimens of *C. albidus* are not available for study and so it is not possible to state emphatically that it either was or was not cementing at the time of death. Further investigation is obviously required to test this hypothesis.

The form of the cement is interesting and there are similarities with observations on the remarkable arenaceous coatings on the outside of two veneroid bivalves of the genera *Granicorium* and *Samarangia* (Taylor et al., 1999). These authors showed that sand grains were attached to one another and to the shell by a crystalline aragonitic cement, with a texture strikingly similar to early diagenetic marine cements. The crystals had grown in mucus secreted at the ventral valve edge, probably mediated by the action of bacteria, which were also visible in their published micrographs. It seems likely that mucus secreted between the periostracum of *Cleidotherus albidus* and the substratum forms a similar environment for the growth of a cement. Where this process is advanced, spherulitic areas of cement are developed. Fixation of our specimens is probably not good enough to determine the presence of bacteria associated with the cement.

It is of interest to consider the evolution of cementation within the Pandoroidea. It seems that both *Cleidotherus* and *Myochama* use similar methods of cementation. There is no doubt, however, that they are not sister-taxa; *Myochama* clearly evolved from the geologically older, free-living, co-familial *Myadora* and it is clear, therefore, that the cemented habit has evolved twice within the Pandoroidea. Since both clades have similar first appearance dates in the fossil record (*Cleidotherus* in the Lower Miocene and *Myochama* in the Upper Oligocene [Beu and Maxwell, 1990]) and overlapping geographic distributions, it is tempting to speculate that the cemented habit arose in response to the same selection pressures. This seems unlikely, however, since *Myochama*, although capable of cementing to open rock surfaces, will only do so after considerable delay, presumably when the preferred substratum, i.e. the posterior end of living infaunal bivalves, are not available (Harper and Morton, 2000).



## Acknowledgements

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## Key to abbreviations used in the figures

|        |  |
|--------|--|
| C      | Craters where individual sand grains are reflected on the cemented scar. |
| FIMF   | Fused inner and middle (inner surfaces) mantle folds                     |
| HA     | Haemocoel  |
| IP(L)  | Inner layer of periostracum (left mantle lobe)                           |
| IP(R)  | Inner layer of periostracum (right mantle lobe)                          |
| M      | Mantle   |
| N      | Nacre  |
| OE     | Outer epithelium   |
| OMF(L) | Left outer mantle fold   |
| OMF(R) | Right outer mantle fold  |
| OMF(1) | Outer component of the outer mantle fold                                 |
| OMF(2) | Inner component of the outer mantle fold                                 |
| OP(L)  | Outer layer of periostracum (left valve)                                 |
| OP(R)  | Outer layer of periostracum (right valve)                                |
| P      | Periostracum   |
| PI     | Prodissoconch I  |
| PII    | Prodissoconch II   |
| PR     | Prismatic outer shell layer  |
| PEG(1) | Outer element of the periostracal groove                                 |
| PEG(2) | Inner element of the periostracal groove                                 |
| PN     | Pallial nerve  |
| PRM(1) | Inner element of the pallial retractor muscles                           |
| PRM(2) | Outer element of the pallial retractor muscles                           |
| S      | Sandstone substratum   |
| SC1    | Secretory cell Type 1  |
| SC2    | Secretory cell Type 2  |
| TF     | Transverse fibres  |

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